Available online at www.sciencedirect.com
SCIENCE DIRECT®
ELSEVIER
Small Ruminant Research 57 (2005) 175–186
Small Ruminant Research
www.elsevier.com/locate/smallrumres

Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Rambouillet sheep☆

K.J. Hanford[a,*], L.D. Van Vleck[b], G.D. Snowder[c,1]

[a] *Department of Animal Science, A218 Animal Science, University of Nebraska, Lincoln, NE 68583-0908, USA*
[b] *USDA, ARS, US Meat Animal Research Center, Lincoln, NE 68583-0908, USA*
[c] *USDA, ARS, US Sheep Experiment Station, Dubois, ID 83423, USA*

Received 7 January 2004; received in revised form 15 June 2004; accepted 12 July 2004

Abstract

Records were for Rambouillet sheep from data collected from 1950 to 1998 at the U.S. Sheep Experiment Station, Dubois, Idaho, USA. Number of observations were 44,211 for litter size at birth and litter size at weaning, 35,604 for birth weight, 34,114 for weaning weight, 39,820 for fleece weight, 39,821 for fleece grade, and 3574 for staple length. Genetic parameters from both single- and two-trait analyses for prolificacy, weight, and wool traits were estimated using REML with animal models. Direct heritability estimates from single-trait analyses were 0.09 for litter size at birth, 0.06 for litter size at weaning, 0.27 for birth weight, 0.20 for weaning weight, 0.51 for fleece weight, 0.16 for fleece grade, and 0.58 for staple length. Estimates of direct genetic correlation between litter sizes at birth and weaning was 0.76 and between birth and weaning weights was 0.60. Estimates of genetic correlation between fleece weight and staple length was positive (0.45), but negative between fleece weight and fleece grade (−0.47) and between staple length and fleece grade (−0.52). Estimates of genetic correlations were near zero between birth weight and litter size at weaning, small and positive between birth weight and litter size at birth, and moderate and positive between weaning weight and litter size traits. Fleece weight, fleece grade, and staple length were slightly but negatively correlated with both litter size traits. Estimates of correlations between weight traits and fleece weight were positive and low to moderate. Estimates of correlations between weight traits and fleece grade were negative and small, while estimates between weight traits and staple length were positive and small. Breeding values from both single- and seven-trait analyses calculated using the parameters estimated from the single- and two-trait analyses were compared across years of birth with respect to genetic trends. Estimated breeding values averaged by year of birth from both the single- and seven-trait analyses for the prolificacy and weight traits increased over time, while those for fleece weight decreased and those for the other wool traits were unchanged. Estimated changes in breeding values over time did not differ substantially for the single- and seven-trait analyses, except for

☆ Published as paper no. 14469, Journal Ser., Nebraska Agric. Res. Div., Univ. of Nebraska, Lincoln 68583-0908.

* Corresponding author. Tel.: +1 402 472 6409; fax: +1 402 472 6362.
E-mail address: khanford2@unl.edu (K.J. Hanford).
[1] Present address: Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933-0166, USA.

doi:10.1016/j.smallrumres.2004.07.003

traits highly correlated with another trait that was responding to selection (i.e., litter size at birth, which was highly correlated to both litter size at weaning and weaning weight).

Keywords: Genetic correlation; Heritability; Litter size; Prolificacy; Weaning weight

1. Introduction

Few long-term selection studies have been conducted with dual-purpose Western range sheep in the U.S. Lasslo et al. (1985) reported genetic improvement in Targhee sheep selected for weaning weight over 20 years, in a range environment. Burfening et al. (1993) found that 18 years of selection based on a reproductive index of lifetime number of lambs born resulted in a favorable response in Rambouillet range ewes. Ercanbrack and Knight (1998) showed that selection solely for litter weight of lamb weaned substantially increased lamb production with only minor penalties in wool production for four breeds of range sheep selected for a 12-year period. Although Sakul et al. (1999) reported only slight improvement in litter size and 120-day weight over a 30-year period for Targhee sheep in a range environment, the authors concluded that the response represented a potentially significant economic advantage. Analyses of Columbia and Targhee sheep selected concurrently with the Rambouillet sheep summarized in this paper indicated that both Columbia and Targhee sheep respond favorably to selection for weaning performance (Hanford et al., 2002, 2003).

The objective of this study was to document genetic trends in production traits of the Rambouillet breed at the United States Sheep Experiment Station (USSES), Dubois, Idaho, USA, over a 49-year period (1950–1998), where selection has been based on weaning performance under range conditions. The traits analyzed included prolificacy, weight, and wool traits. Another objective was to compare genetic trends for each trait estimated from either a single-trait analysis or from a seven-trait analysis.

2. Materials and methods

2.1. Animals and management

The Rambouillet breed, although originally developed in France as a wool breed, after importation in the mid 1800s (Dickson and Lush, 1933), was developed into a dual-purpose breed in the U.S. (Hultz and Hill, 1931). The Rambouillet was the foundation of most Western U.S. range flocks (Wentworth, 1948). The Rambouillet breed has been maintained and included in a variety of selection projects at the USSES (Ercanbrack and Knight, 1981, 1998) and is one of the foundation breeds used in development of the Columbia, Targhee and Polypay breeds (Terrill, 1947; Wentworth, 1948; Hulet et al., 1984). This population of Rambouillet sheep represents the longest time span (49 years) and the largest number of animals (approximately 44,000 lamb records) currently available for determining genetic parameters for the Rambouillet breed. Currently, few estimates of genetic parameters for the Rambouillet breed are available. Bromley et al. (2000) estimated genetic parameters using data collected from 1977 to 1996 from this population.

For 49 years (1950–1998), the Rambouillet breed at USSES was subjected to different selection criteria, all generally related to increasing weaning weight. Early in the period studied, selection favored wool and growth traits (approximately 1950–1969), followed by selection for individual lamb weaning weight and litter size (1969–1976), for weaning weight of the lamb or total litter weight weaned of the ewe (1976–1992) and finally for wool or total litter weight weaned (1992–1998). For many of these years, a random bred control line was also maintained. Lines were re-randomized when new selection criteria were imposed. Rams in control lines that were superior for the selection traits were often used in the appropriate selection lines. The effects of specific selection objectives could not be accounted for because of the re-randomization of breeding animals over the years of this study. The genetic trend in this flock, however, may represent general, but changing, selection emphases of the American sheep industry over this time period.

The number of records per trait, as well as unadjusted means and standard deviations, are presented in Table 1. Ercanbrack and Knight (1998) and Hanford

Table 1
Number of records, animals with records, sires and dams of animals with records, years of records, and unadjusted means and standard deviations of prolificacy, weight, and wool traits

Trait	Records	Animals with records	Sires	Dams	Years of record	Mean ± S.D.
Prolificacy traits (trait of ewe)						
Litter size at birth[a]	44211	12306	1648	5806	1950–1998	1.33 ± 0.69
Litter size at weaning[a]	44211	12306	1648	5806	1950–1998	0.97 ± 0.70
Weight traits (trait of lamb)						
Birth weight (kg)	35604	35604	1830	9484	1950–1998	4.68 ± 0.77
Weaning weight (kg)	34114	34114	1829	9384	1950–1998	32.3 ± 5.4
Wool traits (trait of ewe)						
Fleece weight (kg)	39820	11153	1637	5699	1953–1998	4.65 ± 0.91
Fleece grade, U.S. spinning count[b]	39821	11153	1637	5699	1953–1998	63.2 ± 2.1
Staple length (cm)	3574	3574	495	1903	1977–1991	7.74 ± 0.95

[a] Includes records from all ewes exposed to a ram at breeding and present at lambing.
[b] Spinning counts equivalence to micron system: 60 = 23.50–24.94; 62 = 22.05–23.49; 64 = 20.60–22.04; 70 = 19.15–20.59.

et al. (2002) previously described management of the flock.

2.1.1. Prolificacy traits

Lambs were born primarily in April. Litter size at birth (number of lambs born per ewe exposed in single-sire pen matings) and litter size at weaning (number of lambs weaned per ewe exposed) were recorded for each ewe exposed and present at lambing. Only lambs raised by their dam were included in litter size at weaning. Number of litters and survival are presented by the type of birth in Table 2. Number of ewes, litter size at both birth and weaning, and survival are presented by age of ewe at lambing in Table 3.

2.1.2. Weight traits

Birth weight (kg) was recorded for all lambs born alive. Only records from purebred lambs raised by their birth dam were included in analyses of weaning weight data. Weaning weight (kg) was adjusted to 120 days of age, using individual birth weight and ADG from birth to weaning.

Table 2
Number of litters of ewes bred and present at lambing and unadjusted survival rates (percentage of lambs born) at birth and weaning by type of birth

Birth type	Number of litters (% of total)	Survival	
		Birth	Weaning
Nonpregnant	4395 (9.9)	–	–
Singles	21851 (49.4)	90.1	76.6
Twins	16823 (38.0)	94.8	72.7
Triplets	1120 (2.5)	88.8	48.4
Quadruplets	22 (0.1)	90.9	30.6

2.1.3. Wool traits

Annual greasy fleece weight (kg) and fleece grade (U.S. spinning count) were obtained at shearing in late May. Fleece grades were subjectively determined by certified graders according to U.S. wool grade standards (Pohle, 1963). Staple length (cm) was measured prior to shearing at midside without stretching the fiber. Staple length was primarily measured on yearlings. Staple lengths for yearling ewes were available from 1977 to 1991. Only wool data from ewes with lambing records were included in these analyses.

2.2. Statistical analysis

(Co)variance components were estimated from single-trait analyses using models described in Table 4. (Co)variance components between traits were estimated from two-trait analyses with the models described in Table 4 combined with appropriate covariances between random effects in the model for the pairs of traits. Breeding values of individual animals were estimated from single-trait analyses and were also estimated from a seven-trait analysis, using the within trait co(variances) from single-trait analyses and between trait covariances from two-trait analyses. Means of estimated breeding values by year of birth were calculated from the seven-trait analysis and compared with the corresponding means of estimated breeding values from single-trait analyses.

Table 3
Number of litters and unadjusted litter sizes of ewes bred and present at lambing and survival rates (percentage of lambs born) at birth and weaning (120 days) by age of ewe at lambing

Age (years)	Number of ewes (% of total)	Number of litters	Litter size[a]		Survival	
			Birth	Weaning	Birth	Weaning
1	3977 (9.0)	2272	0.65	0.40	90.8	64.5
2	10119 (22.9)	9201	1.12	0.79	90.6	71.9
3	8642 (19.6)	8105	1.37	1.00	90.1	74.7
4–6	16913 (38.3)	16022	1.55	1.16	93.7	76.7
≥7	4560 (10.3)	4214	1.54	1.09	93.9	72.9

[a] Includes records from all ewes exposed to a ram at breeding and present at lambing.

Fixed factors shown in Table 4 are the same as were used with the analyses of the Columbia (Hanford et al., 2002) and Targhee (Hanford et al., 2003) breeds. For two-trait analyses for litter size at weaning with each of the wool traits, the fixed effect of number of lambs weaned included in the model for wool traits was dropped from the model due to apparent confounding with litter size at weaning.

For the two-trait analyses, correlations between permanent environmental effects were estimated between prolificacy traits and wool traits recorded in the same year of production. Estimates of environmental correlations between a ewe's own birth weight, weaning weight, and yearling staple length and her prolificacy and wool traits were calculated with the formula presented by Okut et al. (1999), which forces

Table 4
Description of fixed and random factors in animal models associated with prolificacy, weight, and wool traits

Trait	Fixed factors	Random factors	Covariate
Litter size at birth	Year of reproduction Age of ewe (years)	Direct genetic (ewe) Permanent environmental (ewe)	
Litter size at weaning	Year of reproduction Age of ewe (years) Foster code[a]	Direct genetic (ewe) Permanent environmental (ewe)	
Birth weight (kg)	Year of birth Age of dam (years) Gender of lamb Type of birth	Direct genetic (lamb) Maternal genetic (dam) Permanent environmental (dam)	
Weaning weight (kg)	Year of birth Age of dam (years) Gender of lamb Type of birth and rearing[b]	Direct genetic (lamb) Maternal genetic (dam) Permanent environmental (dam)	
Fleece weight (kg)	Year of production Age of ewe (years) Number of lambs weaned[c]	Direct genetic (ewe) Permanent environmental (ewe)	Day of year shorn
Fleece grade, U.S. spinning count	Year of production Age of ewe (years) Number of lambs weaned[c]	Direct genetic (ewe) Permanent environmental (ewe)	Day of year shorn
Staple length (cm)	Year of production Number of lambs weaned[c]	Direct genetic (yearling ewe)	Day of year shorn

[a] Foster code: 1, if ewe did not raise a foster lamb; 2, if ewe did raise a foster lamb.
[b] One of eight types of birth and rearing combinations was assigned to each lamb to account for a lamb born as a single, twin, triplet, or quadruplet, and reared as a single, twin, or triplet.
[c] For two-trait analyses with litter size at weaning, number of lambs weaned was dropped from the model.

the covariance between environmental effects into the covariance between permanent environmental effects rather than to the covariance between residual effects when one of the traits is measured more than once. The environmental variance for the single-measured trait was calculated by summing variance components for permanent environmental and temporary environmental effects. For pairs of traits measured in the same year for each ewe (litter size at birth, litter size at weaning, fleece weight, and fleece grade), covariances between both permanent and temporary environmental effects were estimated from two-trait analyses.

To estimate breeding values jointly for seven traits, estimates of (co)variances from single-trait analyses and estimates of covariances from two-trait analyses were used for the mixed model equations. A 9×9 genetic (co)variance matrix and an 11×11 environmental (co)variance matrix were constructed. If the permanent environmental effect was completely confounded with the temporary environmental effect, a fraction of the total environmental variance (0.0001) was arbitrarily assigned to the temporary environmental variance for traits measured only once and the remainder was assigned to the permanent environmental variance (Hanford et al., 2003). Each (co)variance matrix had to be adjusted to be positive definite by applying singular value decomposition to each of the two matrices (Hanford et al., 2003).

A derivative-free REML algorithm (DFREML, Graser et al., 1987) using computer programs of Boldman et al. (1995) was used to estimate (co)variance components. Local convergence was defined as when the variance of the -2 log-likelihoods in the simplex was less than 10^{-6}. Global convergence was considered attained when the -2 log-likelihoods did not change to the third decimal after restarting.

3. Results and discussion

3.1. Estimates from single-trait analyses

Estimates of genetic parameters from single-trait analyses for prolificacy, weight, and wool traits are given in Table 5. Except where noted, estimates of genetic parameters were similar to those reported for Columbia and Targhee, which were contemporaries of the Rambouillet at USSES (Hanford et al., 2002, 2003).

3.1.1. Prolificacy traits

Heritability estimates were small, 0.09 for litter size at birth and 0.06 for litter size at weaning. Fractions of variance due to permanent environmental effects of the ewe were also small, 0.05 for both litter size traits. The estimates are similar to estimates previously reported for dual-purpose breeds for both litter size at birth and

Table 5
Estimates of genetic parameters and standard errors from single-trait analyses[a]

Trait	h_a^2	h_m^2	r_{am}	p^2	e^2	σ_p^2
Prolificacy traits (trait of ewe)						
Litter size at birth	0.09 ± 0.01	ND[b]	ND[b]	0.05 ± 0.01	0.87 ± 0.01	0.358
Litter size at weaning	0.06 ± 0.01	ND[b]	ND[b]	0.05 ± 0.01	0.90 ± 0.01	0.380
Weight traits (trait of lamb)						
Birth weight (kg)	0.27 ± 0.02	0.19 ± 0.01	0.03 ± 0.04	0.07 ± 0.01	0.46 ± 0.01	0.397
Weaning weight (kg)	0.20 ± 0.01	0.10 ± 0.01	0.33 ± 0.07	0.04 ± 0.01	0.60 ± 0.01	19.5
Wool traits						
Fleece weight (kg)	0.51 ± 0.01	ND[b]	ND[b]	0.11 ± 0.01	0.38 ± 0.01	0.607
Fleece grade, spinning count	0.16 ± 0.01	ND[b]	ND[b]	0.07 ± 0.01	0.77 ± 0.01	2.97
Staple length (cm)	0.58 ± 0.03	ND[b]	ND[b]	ND[c]	0.42 ± 0.03	0.722

[a] h_a^2: direct heritability; h_m^2: maternal heritability; r_{am}: correlation between direct and maternal genetic effects; p^2: variance due to permanent environmental effects associated with the animal as proportion of total variance, where the animal is the ewe for ewe traits and the dam for lamb traits; e^2: variance due to residual effects as proportion of total variance; σ_p^2: phenotypic variance.

[b] Maternal effects not included in the model for traits of the ewe.

[c] Permanent environmental effects not included for staple length because the trait was measured only once at 1 year of age.

at weaning (Burfening et al., 1993; Safari and Fogarty, 2003) and to estimates for lambs born per parturition and lambs weaned per parturition (de Vries et al., 1998; Sakul et al., 1999). The heritability estimate for litter size at weaning is similar to the realized heritability estimate for survival to weaning reported by Bradford et al. (1999) for grade Targhee ewes.

3.1.2. Weight traits

Estimates of direct heritability were moderate for both birth weight (0.27) and weaning weight (0.20). The estimate of maternal heritability for birth weight was nearly twice as large as for weaning weight (0.19 versus 0.10). Estimates of genetic correlation between direct and maternal effects were near zero for birth weight (0.03) and moderate for weaning weight (0.33). As a proportion of total variance, estimates of variance due to permanent environmental effects associated with the dam were similar for birth weight (0.07) and weaning weight (0.04). Estimates for direct and maternal heritabilities for weaning weight were similar to the estimates of 0.22 and 0.11, respectively, reported for Targhee (Hanford et al., 2003), but were greater than the estimates of 0.16 and 0.08 reported for Columbia (Hanford et al., 2002). The estimate of direct heritability for birth weight was within the range of estimates for dual-purpose breeds compiled by Safari and Fogarty (2003) of 0.03–0.41, but greater than the estimate of 0.13 reported by Jurado et al. (1994). The estimate of direct heritability for weaning weight was in general agreement with the range of estimates (0.10–0.45) for dual-purpose breeds for weaning weights measured between 100 days and 4 months (Safari and Fogarty, 2003) and to the estimate of 0.19 reported by Al-Shorepy and Notter (1996) for 120 days weight. The larger estimate of maternal heritability for birth weight compared with the estimate for weaning weight supports the conclusion of Robison (1981) that maternal genetic effects generally are important for measurements of weight at younger ages and diminish with increasing age. This diminishing maternal genetic effect on lamb weight over time has also been reported by others (Al-Shorepy and Notter, 1996; Näsholm and Danell, 1996).

3.1.3. Wool traits

Estimates of direct heritability were 0.51, 0.16, and 0.58, for fleece weight, fleece grade, and staple length, respectively. These estimates are similar to those reported for fleece weight and staple length for Columbia and Targhee by Hanford et al. (2002, 2003), but the estimate for fleece grade was smaller than the 0.41 reported for both breeds. The estimate for fleece weight was on the higher end of the range of estimates (0.15–0.55) for dual-purpose breeds (Safari and Fogarty, 2003), but smaller than the 0.60 reported by Saboulard et al. (1995) for clean fleece weight in western white-face ewes. The estimate for fleece grade was smaller than any of the estimates (0.18–0.75) for dual-purpose breeds compiled by Safari and Fogarty (2003). Hillers and Everson (1972) and Roff (2001) reported heritability estimates from traits with discrete measures to be consistently smaller than heritability estimates from continuous data. Spinning count is measured discretely but fiber diameter is measured on a continuous scale (Safari and Fogarty, 2003). Estimates of variance as a proportion of total variance due to permanent environmental effects of the ewe were 0.11 for fleece weight and 0.07 for fleece grade.

3.2. Estimates from two-trait analyses

Estimates of genetic correlations from two-trait analyses among and within groups of prolificacy, weight and wool traits are presented in Table 6. Except where noted, the estimates were in good agreement with the estimates reported for the contemporary Columbia and Targhee by Hanford et al. (2002, 2003).

3.2.1. Within prolificacy traits

The estimate of direct genetic correlation between litter size at birth and litter size at weaning was large and positive (0.76) and within the range of estimates (0.29–1.00) reviewed by Safari and Fogarty (2003).

The estimate of correlation between permanent environmental effects of ewes was moderate and positive for litter size at birth with litter size at weaning (0.57) and was similar to the estimate of 0.52 reported for Columbia but somewhat smaller than the estimate of 0.73 reported for Targhee (Hanford et al., 2002, 2003).

3.2.2. Within weight traits

The estimate of direct genetic correlation between birth and weaning weights was moderate and positive (0.60) and within the range (0.16–0.82) compiled by Safari and Fogarty (2003) between birth weight and

Table 6
Estimates of genetic and environmental correlations from two-trait analyses between prolificacy, weight, and wool traits[a]

Trait 1	Trait 2	r_g	r_m	r_{a1m2}	r_{a2m1}	r_p	r_e
Litter size at birth	Litter size at weaning	0.76				0.57	0.54
Birth weight (kg)	Weaning weight (kg)	0.60	0.36	0.08	0.25	0.36	0.31
Fleece weight (kg)	Fleece grade (count)	−0.47				−0.20	−0.09
Fleece weight (kg)	Staple length (cm)	0.45				ND[b]	0.21
Fleece grade (count)	Staple length (cm)	−0.52				ND[b]	−0.06
Litter size at birth	Birth weight (kg)	0.24		0.06			−0.00
Litter size at birth	Weaning weight (kg)	0.49		0.25			0.07
Litter size at weaning	Birth weight (kg)	0.00		0.27			0.01
Litter size at weaning	Weaning weight (kg)	0.56		0.70			0.03
Litter size at birth	Fleece weight (kg)	−0.08				0.30	−0.12
Litter size at birth	Fleece grade (count)	−0.11				0.09	0.01
Litter size at birth	Staple length (cm)	−0.16				ND[b]	0.05
Litter size at weaning	Fleece weight (kg)	−0.04				0.10	0.11
Litter size at weaning	Fleece grade (count)	−0.10				0.10	0.02
Litter size at weaning	Staple length (cm)	−0.04				ND[b]	0.02
Birth weight (kg)	Fleece weight (kg)	0.21			0.16		0.19
Birth weight (kg)	Fleece grade (count)	−0.15			−0.02		−0.00
Birth weight (kg)	Staple length (cm)	0.14			−0.02		0.13
Weaning weight (kg)	Fleece weight (kg)	0.27			0.11		0.24
Weaning weight (kg)	Fleece grade (count)	−0.14			−0.02		0.00
Weaning weight (kg)	Staple length (cm)	0.09			0.05		0.26

[a] r_g: correlation between direct genetic effects; r_m: correlation between maternal genetic effects; r_{aimj}: correlation between direct additive genetic effect for trait i and maternal genetic effect for trait j; r_p: correlation between permanent environmental effects (maternal between birth weight and weaning weight and direct between prolificacy and wool traits); r_e: correlation between temporary environmental effects.

[b] Permanent environmental effects not included for staple length because the trait was measured only once at 1 year of age.

weaning weight measured between 100 and 120 days. The estimate of maternal genetic correlation between birth weight and weaning weight was also moderately positive (0.36) although somewhat smaller than the estimate of 0.58 and 0.43 reported for Columbia and Targhee (Hanford et al., 2002, 2003) and smaller than the range (0.49–0.93) compiled by Safari and Fogarty (2003). Estimates of genetic correlations between direct and maternal effects were both small to moderate (0.08 and 0.25). The estimate of correlation between permanent environmental effects of the dam for birth and weaning weights was moderate and positive (0.36) and somewhat smaller than estimates of 0.46 and 0.44 for Columbia and Targhee (Hanford et al., 2002, 2003).

3.2.3. Within wool traits

Estimates of direct genetic correlations were positive between fleece weight and staple length (0.45) and negative between fleece grade and both fleece weight (−0.47) and staple length (−0.52), in agreement with previous estimates (Saboulard et al., 1995; Hanford et al., 2002, 2003).

The negative (unfavorable) estimate of the genetic correlation between fleece grade and fleece weight was in general agreement with positive (unfavorable) estimates between fleece fiber diameter and fleece weight previously published (Iman et al., 1992; Safari and Fogarty, 2003). The positive estimate of genetic correlation (0.45) between fleece weight and staple length agreed in direction with the estimate of 0.20 between yearling fleece weight and staple length reported for Merino sheep by Atkins (1997). Although Atkins (1997) reported a negative (favorable) genetic correlation between yearling fiber diameter and staple length (−0.10), the negative (unfavorable) genetic correlation between fleece grade and staple length estimated in this study indicates that staple length would decrease as a genetic response to an increase in fleece grade (fiber diameter becomes finer).

3.2.4. Prolificacy and weight traits

Estimates of genetic correlations among prolificacy and weight traits ranged from 0.00 between litter size at weaning and birth weight to 0.56 between litter size at weaning and weaning weight. The estimate of genetic correlation between litter size at birth and birth weight (0.24) was larger than the 0.10 and 0.00 reported for Columbia and Targhee (Hanford et al., 2002, 2003). The estimate of the genetic correlation between birth weight and litter size at weaning (0.00) was smaller than the estimate (0.34) reported in the review by Fogarty (1995).

The estimate of genetic correlation between weaning weight and litter size at birth (0.49) was larger than estimates of 0.33 and 0.20 reported for Columbia and Targhee (Hanford et al., 2002, 2003). The estimate of genetic correlation between weaning weight and litter size at weaning (0.56) was also larger than the estimates of 0.25 and 0.15 reported for the Columbia and Targhee breeds (Hanford et al., 2002, 2003).

Estimates of correlations between direct genetic effects for prolificacy traits and maternal genetic effects for weight traits ranged from 0.06 between litter size at birth and birth weight to 0.70 between litter size at weaning and weaning weight, which were in general agreement with the estimates for Columbia and Targhee (Hanford et al., 2002, 2003).

3.2.5. Prolificacy and wool traits

All estimates of genetic correlations between prolificacy traits and wool traits were negative and small, ranging from −0.16 between litter size at birth and staple length to −0.04 between litter size at weaning and both fleece weight and staple length. Hanford et al. (2002, 2003) reported between litter sizes at birth and weaning and fleece grade small positive correlations for both Columbia (0.17 and 0.04, respectively) and Targhee (0.09 and 0.11, respectively). The finer wool grade of the Rambouillet breed (average 63.2 count) appears to be more adversely affected by increases in prolificacy than either Columbia or Targhee, with average grade counts of 55.9 and 60.2, respectively (Hanford et al., 2002, 2003).

3.2.6. Weight and wool traits

Estimates of genetic correlations ranged from −0.15 between birth weight and fleece grade to 0.27 between weaning weight and fleece weight. Positive correlations for fleece weight with birth and weaning weight (0.21 and 0.27, respectively), suggest some genetic factors influencing animal growth may also influence wool growth.

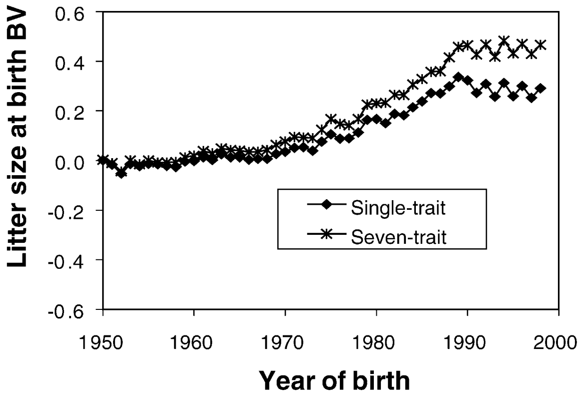

Fig. 1. Means of estimates of breeding value (BV) for litter size at birth by year of birth from single- and seven-trait analyses.

3.3. Estimates of genetic change

Means of estimates of breeding value by year of birth calculated from single-trait analyses and from the seven-trait analysis are plotted in Figs. 1 and 2 for prolificacy traits, in Figs. 3 and 4 for weight traits, and in Figs. 5–7 for wool traits. The means are deviations from the means of estimates of breeding value for animals born in 1950 (1977 for staple length). Except where noted, results were similar to those reported for the contemporary Columbia and Targhee by Hanford et al. (2002, 2003).

3.3.1. Prolificacy traits

Means of estimates of breeding value by year of birth for litter size at birth from the single-trait analysis

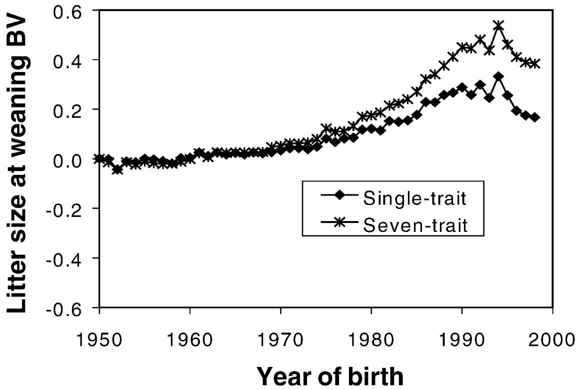

Fig. 2. Means of estimates of breeding value (BV) for litter size at weaning by year of birth from single- and seven-trait analyses.

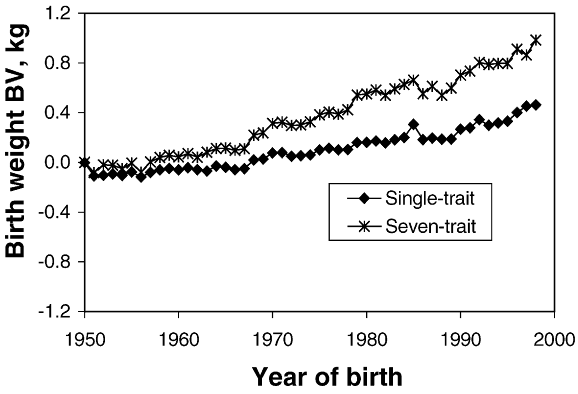

Fig. 3. Means of estimates of breeding value (BV) for birth weight of lambs by year of birth from single- and seven-trait analyses.

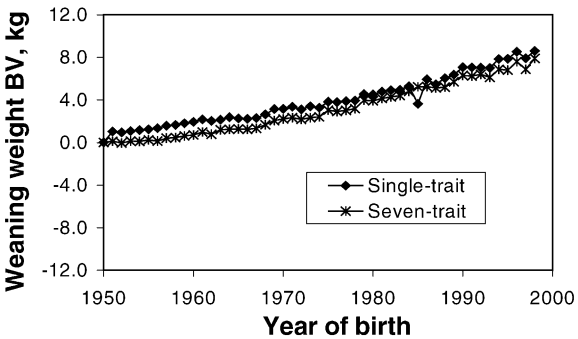

Fig. 4. Means of estimates of breeding value (BV) for weaning weight of lambs by year of birth from single- and seven-trait analyses.

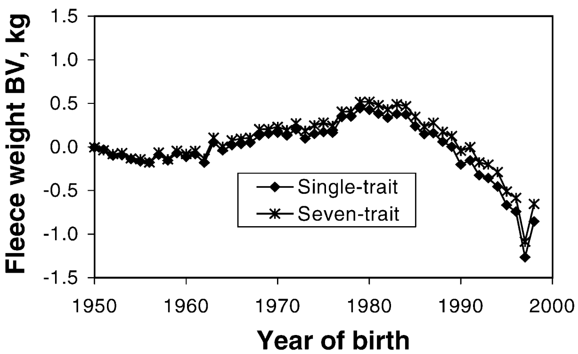

Fig. 5. Means of estimates of breeding value (BV) for fleece weight of ewes and ewe lambs by year of birth from single- and seven-trait analyses.

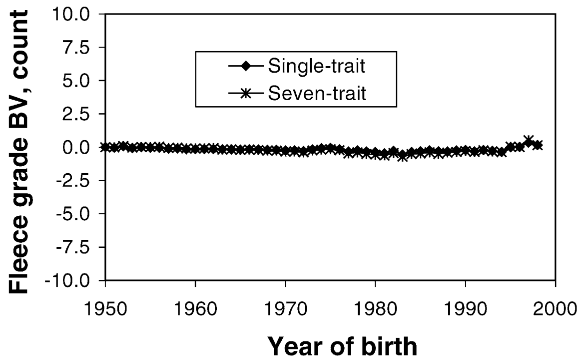

Fig. 6. Means of estimates of breeding value (BV) for fleece grade of ewes and ewe lambs by year of birth from single- and seven-trait analyses.

and the seven-trait analysis were similar from 1950 to 1980 (Fig. 1). From 1980 to 1990, average estimates of breeding values from the seven-trait analysis increased at a greater rate than average estimates from the single-trait analysis, so that by 1990, the average estimate of breeding value from the seven-trait analysis was 0.2 lambs greater than from the single-trait analysis. This difference for litter size at birth may be due to the positive direct correlations between litter size at birth and both litter size at weaning (0.76) and weaning weight (0.56) which both increased. From 1990 to 1998, average estimates from both the single- and seven-trait analyses for litter size at birth did not increase. The mean estimates for litter size at birth increased about 0.4 lambs from 1950 to 1998. Differences between

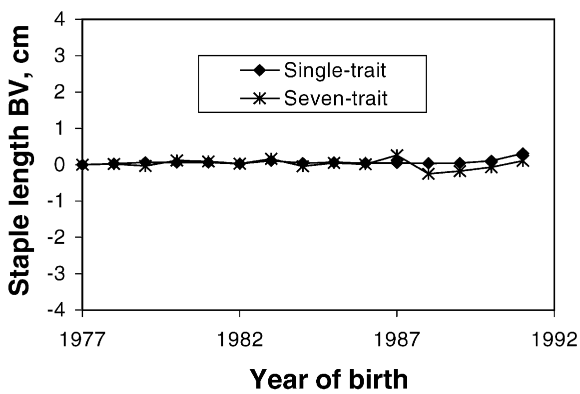

Fig. 7. Means of estimates of breeding value (BV) for staple length of ewe lamb fleeces by year of birth from single- and seven-trait analyses by year of birth.

the single- and seven-trait analyses were less for both Columbia and Targhee (Hanford et al., 2002, 2003). These differences among the breeds could be due to the smaller estimates of direct correlation between litter size at birth and weaning weight (0.33 and 0.20, respectively, for Columbia and Targhee).

Means of estimates of breeding value by year of birth for litter size at weaning from the single- and the seven-trait analyses also were similar from 1950 to 1980 (Fig. 2). From 1980 to 1992, average estimates of breeding values from the seven-trait analysis increased at a greater rate than average estimates from the single-trait analysis, so that by 1992, the average estimate of breeding value from the seven-trait analysis was 0.2 lambs greater than from the single-trait analysis. This 0.2 lamb difference was maintained from 1992 to 1998, even though the average estimates of breeding values declined by 0.2 lambs during this period. The mean of estimates of breeding value for litter size at weaning increased by 0.4 lambs during the study period, which was similar to the increase for litter size at birth. Except for the decline from 1992 to 1998, the plot of the mean estimates of breeding value by year of birth for litter size at weaning was similar to that for the Targhee (Hanford et al., 2003), with the average estimates from the seven-trait analysis greater than those from the single-trait analysis. However, the pattern was different for the Columbia (Hanford et al., 2002), for which the average estimates of breeding value calculated from the single-trait analysis were greater than the average estimates of breeding value calculated from the seven-trait analysis, which was thought to be due partly to the introduction of outside Columbia rams, which negatively impacted weaning weight, which, in turn, was correlated with litter size at weaning (0.24).

3.3.2. *Weight traits*

Means of estimates of breeding value for birth weight by year of birth from the single-trait analysis were slightly less from 1951 to 1957 than means of estimates of breeding value from the seven-trait analysis (Fig. 3). During that period, the average estimate of breeding value for birth weight was close to zero. The differences between means of estimates of breeding value from single- and seven-trait analyses steadily increased from 1957 to 1998 to a difference of over 0.6 kg. Selection had not been applied directly for birth weight. The final 0.6 kg difference between the two means of estimates of breeding value for birth weight may be due to the positive genetic correlations between birth weight and litter size at birth (0.24). Means of estimates of breeding value for birth weight from the single- and seven-trait analyses increased about 0.4 and 1.0 kg, respectively, during the study period. The plot was different from the pattern of plots for Columbia and Targhee (Hanford et al., 2002, 2003). Differences between the mean estimates from single- and seven-trait analyses for these two breeds were less and probably related to smaller estimates of genetic correlation between birth weight and litter size at birth (0.10 and 0.00, respectively, for Columbia and Targhee).

Means of estimates of breeding value for weaning weight by year of birth from single-trait analysis were slightly greater during the entire study period than means of estimates of breeding value from the seven-trait analyses, with the exception of 1985 (Fig. 4). During the 49-year period, the mean of estimates of breeding value increased about 9.0 kg. Plots of the mean estimates by year of birth for weaning weight followed a pattern different from the patterns from single- and seven-trait analyses for Columbia and Targhee, for which the seven-trait means were slightly greater than the single-trait means (Hanford et al., 2002, 2003). Birth weights for both Columbia and Targhee had increased more over the study period (0.8 and 0.6 kg, respectively) than for the Rambouillet (0.4 kg). The smaller increase for the Rambouillet for birth weight, which is highly correlated to weaning weight (0.60), may have contributed to the difference in estimates of genetic change for weaning weight between the Rambouillet and the other two breeds.

3.3.3. *Wool traits*

Means of estimates of breeding value for fleece weight by year of birth from single- and seven-trait analyses showed a fairly consistent pattern with means of estimates from the seven-trait analysis being slightly greater than means from the single-trait analysis (Fig. 5). The larger means of estimates of breeding value from the seven-trait analysis may be due to the large negative genetic correlation of −0.47 between fleece weight and fleece grade and small positive correlations between fleece weight and both birth weight (0.21) and weaning weight (0.27). Means of estimates of breeding value for fleece weight did not vary much from the base year to 1976. From 1976 to 1980 the means of estimates of breeding value increased by 0.5 kg from the base year. Means then varied between 0.4 and 0.5 kg heavier than the base year until about 1984, when means of estimates of breeding value began a decrease to 1.3 kg below the base year by 1997, although rebounding to only 0.6 kg below the base year estimates in 1998. The overall decrease from the base year for fleece weight was similar to the overall decrease of 0.3 kg reported for the Targhee (Hanford et al., 2003), but different from the 0.3 kg increase reported for the Columbia (Hanford et al., 2002).

Means of estimates of breeding value by year of birth for fleece grade were similar for single- and seven-trait analyses (Fig. 6) with differences of less than 1 spinning count from the base year throughout the study period. Plots of the means by year of birth for fleece grade followed a pattern similar to those from single- and seven-trait analyses for Columbia and Targhee (Hanford et al., 2002, 2003).

Means of estimates of breeding value by year of birth for staple length were similar for single- and seven-trait analyses (Fig. 7) with differences of less than 0.5 cm from the base year throughout the study period. The plots of the mean estimates of breeding value by year of birth for staple length followed a pattern similar to those for the Targhee (Hanford et al., 2003), but a pattern different from that for the Columbia (Hanford et al., 2002). For the Columbia breed, the yearly means of breeding values from the seven-trait analysis were greater than those from the single-trait analysis, which was thought to be due to the high correlation between staple length and fleece weight (0.55) and the increase in fleece weight of the Columbia during the study period.

Averages by year of birth did not appear to differ substantially between estimates of breeding values obtained from single- and seven-trait analyses for traits not highly correlated with other traits that responded to selection. Estimates of breeding value for litter size at birth and litter size at weaning from the seven-trait analysis tended to be greater than estimates from single-trait analyses, which may be due to the high genetic correlation between the traits (0.77). Estimates of breeding value for birth weight and weaning weight from the seven-trait analysis also increased more than estimates from single-trait analyses, which might be due to the high genetic correlation between the traits (0.52). Estimates of genetic correlations less than 0.5 did not have a noticeable impact on means of estimates of breeding value of other traits.

4. Implications

Results from this study agree with those of the previous studies of the Columbia and Targhee breeds (Hanford et al., 2002, 2003), that multiple-trait analyses should be used rather than single-trait analyses when estimating genetic changes because of the impact including correlated traits has on estimates of breeding values of other traits. Selection based on weaning performance over a long period could result in a moderate positive response in both litter size at weaning and weaning weight in flocks of dual-purpose breeds, such as the Rambouillet, Targhee and Columbia. Although litter size at birth and birth weight are lowly heritable, positive genetic correlations between both of these traits and weaning weight and litter size at weaning, which are components of weaning performance, suggest that selecting for weaning performance would result in positive genetic gains in both litter size at birth and birth weight. Although most of the genetic correlations between wool traits and weaning performance were in an undesirable direction, the correlations were also low. Selection for increased weaning performance would offset decreases in wool traits under today's market prices (Snowder, 2002).

References

Al-Shorepy, S.A., Notter, D.R., 1996. Genetic variation and covariation for ewe reproduction, lamb growth, and lamb scrotal circumference in a fall-lambing sheep flock. J. Anim. Sci. 74, 1490–1498.

Atkins, K.D., 1997. Genetic improvement of wool production. In: Piper, L., Ruvinsky, A. (Eds.), The Genetics of Sheep, pp. 471–504.

Boldman, K.G., Kriese, L.A., Van Vleck, L.D., Van Tassell, C.P., Kachman, S.D., 1995. A manual for the use of MTDFREML. A set of programs to obtain estimates of variances and covariances [DRAFT]. ARS-USDA, Clay Center, NE, 114 pp.

Bradford, G.E., Sakul, H., Dally, M.R., 1999. Selection for weaning weight or litter size in range sheep. II. Correlated responses and effect on productivity. Sheep Goat Res. J. 15, 138–146.

Bromley, C.M., Snowder, G.D., Van Vleck, L.D., 2000. Genetic parameters among growth, prolificacy, and wool traits of Columbia, Polypay, Rambouillet, and Targhee sheep. J. Anim. Sci. 78, 846–858.

Burfening, P.J., Kachman, S.D., Hanford, K.J., Rossi, D., 1993. Selection for reproductive rate in Rambouillet sheep: estimated genetic change in reproductive rate. Small Rumin. Res. 10, 317–330.

de Vries, M.J., van der Waaij, E.H., van Arendonk, J.A.M., 1998. Estimation of genetic parameters for litter size in sheep: a comparison of a repeatability and a multivariate model. Anim. Sci. 66, 685–688.

Dickson, W.F., Lush, J.L., 1933. Inbreeding and the genetic history of the Rambouillet sheep in America. J. Heredity 24, 19–33.

Ercanbrack, S.K., Knight, A.D., 1981. Weaning trait comparisons among inbred lines and selected noninbred and randomly bred control groups of Rambouillet, Targhee, and Columbia sheep. J. Anim. Sci. 52, 977–988.

Ercanbrack, S.K., Knight, A.D., 1998. Responses to various selection protocols for lamb production in Rambouillet, Targhee, Columbia, and Polypay sheep. J. Anim. Sci. 76, 1311–1325.

Fogarty, N.M., 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. Anim. Breed. Abstr. 63, 101–143.

Graser, H.-U., Smith, S.P., Tier, B., 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. J. Anim. Sci. 64, 1362–1370.

Hanford, K.J., Van Vleck, L.D., Snowder, G.D., 2002. Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Columbia sheep. J. Anim. Sci. 80, 3086–3098.

Hanford, K.J., Van Vleck, L.D., Snowder, G.D., 2003. Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Targhee sheep. J. Anim. Sci. 81, 630–640.

Hillers, J.K., Everson, D.O., 1972. Effect of various discrete distributions or the magnitude of heritability. J. Dairy Sci. 55, 682 (abstract).

Hulet, C.V., Ercanbrack, S.K., Knight, A.D., 1984. Development of the Polypay breed of sheep. J. Anim. Sci. 58, 15–24.

Hultz, F.S., Hill, J.A., 1931. Range Sheep and Wool in the Seventeen Western States. Wiley, New York.

Iman, N.Y., Johnson, C.L., Russell, W.C., Stobart, R.H., 1992. Estimation of genetic parameters for wool fiber diameter measures. J. Anim. Sci. 70, 1110–1115.

Jurado, J.J., Alonso, A., Alenda, R., 1994. Selection response for growth in a Spanish Merino flock. J. Anim. Sci. 72, 1433–1440.

Lasslo, L.L., Bradford, G.E., Torell, D.T., Kennedy, B.W., 1985. Selection for weaning weight in Targhee sheep in two environments. I. Direct response. J. Anim. Sci. 61, 376–386.

Näsholm, A., Danell, Ö., 1996. Genetic relationships of lamb weight, maternal ability, and mature ewe weight in Swedish finewool sheep. J. Anim. Sci. 74, 329–339.

Okut, H., Bromley, C.M., Van Vleck, L.D., Snowder, G.D., 1999. Genotypic expression at different ages. I. Prolificacy traits of sheep. J. Anim. Sci. 77, 2357–2365.

Pohle, E.M., 1963. Grading and production of wool. In: Wool Handbook. Wiley, New York.

Robison, O.W., 1981. The influence of maternal genetic effects on the efficiency of selection – a review. Livest. Prod. Sci. 8, 121–137.

Roff, P.A., 2001. The threshold model as a general purpose normalizing transformation. Heredity 86, 404–411.

Saboulard, M., Russell, W.C., Riley, M.L., 1995. Selection for lambing rate and clean fleece weight in sheep. J. Anim. Sci. 73, 3195–3198.

Safari, A., Fogarty, N.M., 2003. Genetic parameters for sheep. NSW Agriculture and Australian Sheep Industry, CRC.

Sakul, H., Bradford, G.E., Dally, M.R., 1999. Selection for litter size or weaning weight in range sheep. I. Selection practiced and direct response. Sheep Goat Res. J. 15, 126–137.

Snowder, G.D., 2002. Composite trait selection for improving lamb production. Sheep Goat Res. J. 17, 42–48.

Terrill, C.E., 1947. Breed crosses used in the development of Targhee sheep. J. Anim. Sci. 6, 83–92.

Wentworth, E.N., 1948. America's Sheep Trails. The Iowa State College Press, Ames, IA.